THE CYTOGENETICS OF GENERIC HYBRIDS OF SORBUS

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With one plate

THE POMOIDEAE constitute a group of rather closely related genera of common origin (Sax, 1933). All genera have a basic chromosome number of 17 and generic hybrids are relatively common. Natural hybridization is most frequent between *Sorbus* and the related genera *Aronia, Amelanchier,* and *Pyrus*. Rehder (1940, 1947) has described or enumerated seven hybrids between *Sorbus* and *Aronia* species, three hybrids of *Sorbus* and *Amelanchier,* and one hybrid between *Sorbus* and *Pyrus*. These genera are closely related and have been included in a single genus *Pyrus* by some taxonomists.

The nomenclature in the following descriptions is that of Rehder (1940). The cytological analysis is based upon acetocarmine smear preparations, following fixation in alcohol-acetic acid.

Hybrids between *Sorbus* and *Aronia* include *Sorbaronia Jackii, S. Arsenii, S. hybrida, S. fallax, S. heterophylla, S. alpina,* and *S. Dippelii*. Both the pinnate- and entire-leaved species of *Sorbus* have produced hybrids with *Aronia species,* all of which have entire leaves. *Sorbaronia Dippelii* has been crossed with *Sorbus alnifolia* in the Arnold Arboretum. Three of the *Sorbaronia* hybrids, *S. Jackii, S. alpina,* and *S. Dippelii,* have been examined cytologically and attempts have been made to grow F_2 generations.

Sorbaronia Jackii is a naturally recurring hybrid between *Sorbus americana* and *Aronia prunifolia*. Specimens of the *Sorbus* parent in the Arboretum, both mature trees and 2-year old seedlings, have from 5 to 8 pairs of leaflets with an average number of slightly less than 7. The F_1 hybrid has variable leaves, ranging from entire, as in *Aronia*, to pinnate leaves with as many as 3 pairs of leaflets in addition to the terminal leaflet. Often the leaves are partially pinnate or lobed. The average number of leaflets is 1.4.

The open pollinated progeny of *S. Jackii* are extremely variable in size and viability. Of 50 seedlings selected from the survivors grown in the greenhouse, seven have died in the nursery at the end of the second year, seven are extreme dwarfs, and 36 have made more or less normal growth. All surviving seedlings have at least partially pinnate leaves, ranging from 3 to 7 leaflets with an average of 4.5. No segregates had any entire leaves, but these progeny may be back cross hybrids with adjacent pinnate-leaved species of *Sorbus*. Seedlings of *Sorbus americana* grown in the nursery showed much greater uniformity than those of the hybrid. Of 50 seed-

lings, only one had died at the end of the second year.

Sorbaronia Jackii produces abundant fruits, but much of the seed is defective or produces weak seedlings — pollen sterility is variable, ranging from 0 in some anthers to about 50 per cent in others.

The meiotic divisions were generally irregular, but in some pollen mother cells the divisions appeared to be relatively normal. At first meiotic metaphase there were from 13 to 15 bivalents and from 4 to 8 univalents in most of the figures examined, although the number of univalents ranged from 0 to 12. Lagging univalents were generally found at both first and second anaphase (PL. I, FIG. 1). The tetrads resulting from the two meiotic divisions were often irregular with some micronuclei, but as a rule nearly 50 per cent of the pollen appeared to be morphologically normal.

Sorbaronia alpina is a cross between *Sorbus Aria*, a species with simple leaves, and *Aronia arbutifolia*. This hybrid, as represented by the variety *super-aria*, is more sterile than *Sorbaronia Jackii*. Occasionally there appeared to be 17 bivalent chromosomes at the first meiotic metaphase, but the divisions were generally quite irregular, with as many as 14 lagging univalents at anaphase. For some anaphase figures the lagging chromosomes appeared to include an occasional bivalent (PL. I, FIG. 2). The second meiotic divisions also were irregular and the pollen fertility ranged from 0 to 24 per cent. For both of these *Sorbaronia* hybrids the pollen sterility varied greatly in different flowers and some anthers contained no good pollen. Some fruits are produced by *S. alpina*, but we have not been able to germinate the seeds.

Sorbaronia Dippelii is a hybrid between *Sorbus Aria* and *Aronia melanocarpa*. This hybrid is relatively fertile, as indicated by both pollen sterility and by fruit development. Yet some anthers produce no good pollen and we have not been able to germinate open pollinated seed. Seventeen bivalent chromosomes were found at meiotic metaphase (PL. I, FIG. 3), and there was little irregularity at meiotic anaphase. Pollen development was variable, but some counts showed as high as 58 per cent normal pollen. The pollen fertility of the *Aronia* parent was only 76 per cent and that of the *Sorbus* parent about the same.

We have succeeded in crossing *Sorbaronia Dippelii* with the distinct *Sorbus* species *S. alnifolia*. This hybrid has the characteristic foliage of *S. alnifolia*, the male parent. It is a slow growing shrub and has not yet flowered.

Several hybrids between *Sorbus* and *Amelanchier* have been described. The three known hybrids are growing in the Arnold Arboretum, but only *Amelasorbus Jackii* is large enough to provide meiotic material. This hybrid was found among seedlings grown from seeds collected in the Moscow mountains of Idaho by Professor J. G. Jack. It is described by Rehder as a hybrid between *Sorbus scopulina* and *Amelanchier florida*. According to Professor Jack there were two types of the hybrid, one with partially pinnate leaves and one with only an occasional cleft or lobed leaf. Only the latter type is now available in our collections.

Amelasorbus has been difficult to analyse cytologically. The microspore mother cells appear to disintegrate at any stage of development from prophase to microspores. In favorable prophase preparations 32–34 chromosomes were counted at diakinesis, indicating a very loose association of paired chromosomes. At meiotic metaphase there were from 12 to 15 bivalents and from 4 to 10 univalents (PL. I, FIG. 4). At anaphase the number of lagging univalents are variable, but as many as ten have been observed (PL. I, FIG. 5). Although the meiotic behavior of the chromosomes of *Amelasorbus* is similar to that of two of the *Sorbaronia* hybrids, the sterility is much greater. Practically no normal pollen is formed and very little fruit is produced. Over a period of years only two viable seeds have been obtained and the resulting seedlings, which have now flowered for several years, are very similar to the parental hybrid in both appearance and sterility. Apparently they are of parthenogenetic origin.

Two other forms of *Amelasorbus* are listed by Rehder (1947). *Amelasorbus Hoseri* is thought to be a hybrid between *Sorbus hybrida* and *Amelanchier* sp. It has partially pinnate leaves. *Amelasorbus Raciborskiana* is listed as a cross between *Sorbus* sp. and *Amelanchier asiatica*. It too has partially pinnate leaves. Both of these hybrids were raised at the Kornik Botanical Garden in Poland and named by Wroblewski. Our specimens of these hybrids are not sufficiently mature for meiotic analysis.

The known crosses between *Sorbus* and *Pyrus* are limited to *Sorbopyrus auricularis*, a natural hybrid between *S. Aria* and *P. communis*. We have in the Arnold Arboretum only the variety *bulbiformis*, a form which resembles *Pyrus* in most characters. This hybrid is a triploid with presumably two sets of pear chromosomes. Its cytological behavior has been described earlier (Sax 1932). We have obtained some progeny from open pollinated seeds of *Sorbopyrus*. The seedlings are variable but tend to segregate into two groups — some which are vigorous and resemble the mother tree, and a series of dwarf segregates which survived for one to three years.

In all of these generic hybrids involving *Sorbus* there is considerable sterility, and when segregates are obtained many are weak and do not survive. The genera *Sorbus, Aronia, Amelanchier,* and *Pyrus* can be crossed only in certain combinations. One might suppose that *Aronia* and *Amelanchier* could be crossed, since both have produced at least several hybrids with *Sorbus,* but repeated attempts to cross these genera have failed. However, we also have been unable to produce any artificial hybrids between *Aronia* and *Sorbus,* and yet seven such spontaneous hybrids are known and some are recurrent in nature.

The fact that *Sorbus, Aronia, Amelanchier,* and *Pyrus* can be crossed in certain combination indicates a certain degree of similarity. The behavior of the hybrids does indicate cytogenetic differentiation usually found in diverse species. Whether such incompatibility merits more than specific differentiation is a matter of taxonomic convenience.

SUMMARY

Natural hybrids between *Sorbus* and *Aronia* and between *Amelanchier* and *Pyrus* are partially sterile and show considerable meiotic irregularity. *Sorbaronia* produces a variable progeny both in morphological characters and viability. *Amelasorbus* produces few viable seeds and the progeny appear to be of parthenogenetic origin. *Sorbopyrus* sets few seeds and the progeny include many dwarf segregates which survive for only a few years. The cytogenetic analysis indicates a common origin of these genera, but a degree of differentiation sufficient to maintain generic isolation.

LITERATURE CITED

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EXPLANATION OF THE PLATE

Drawn from acetocarmine preparations. Magnification approximately × 2000.

FIG. 1. *Sorbaronia Jackii.* First meiotic anaphase. FIG. 2. *Sorbaronia alpina super-aria.* First meiotic anaphase. FIG. 3. *Sorbaronia Dippelii.* First meiotic metaphase. FIG. 4. *Amelasorbus Jackii.* First meiotic metaphase. FIG. 5. *Amelasorbus Jackii.* First meiotic anaphase.

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